FIELD OBSERVATIONS ON THE SYMBIOTIC INTERACTIONS OF OGYRIS GENOVEVA (HEWITSON) AND OGYRIS ZOSINE (HEWITSON) (LEPIDOPTERA: LYCAENIDAE) WITH CAMPONOTUS SPP. (HYMENOPTERA: FORMICIDAE)

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Abstract

Observations are presented on the behaviour of Ogyris genoveva and O. zosine and their attendant Camponotus ants.

Introduction

The early stages of *Ogyris genoveva* (Hewitson) and *O. zosine* (Hewitson) have been the subject of a number of biological papers since Miskin (1883) (see Lyell 1905; Waterhouse 1941a, b, Edwards 1948, 1959, McCubbin 1971, Fisher 1978, Common and Waterhouse 1981, Moore 1990, Turner and Hawkeswood 1992). *O. genoveva* occurs throughout most of south-eastern Australia, extending west into South Australia and north into central and northern Queensland, while *O. zosine* occurs over much of northern and eastern Australia, including offshore Barrier Reef and Torres Strait Islands, extending into central and Western Australia (Common and Waterhouse 1981). There are some sympatric populations in south-eastern Queensland and northern New South Wales and both species of *Ogyris* Westwood are almost exclusively attended by ants of the genus *Camponotus* Mayr.

Biological observations have been made by the author over several years and an intensive study was undertaken prior to and during the filming of a documentary on insects, a segment of which was filmed at Eatonsville, west of Grafton, NSW, in November 1993.

Study areas

The principal study site was situated at Eatonsville, extending from approximately 3 km east to 16 km west of the town, where 39 separate colonies of *O. genoveva* were studied in four distinct groups. There were four species of *Camponotus* in attendance, namely *C. consobrinus* (Erichson) (28 colonies), *C. nigriceps* (Smith) (1 colony), *C. eastwoodi* McArthur (1 colony) and *C. intrepidus* (Kirby) (8 colonies), with one unattended. *O. genoveva* and *O. zosine* early stages were also investigated at sites throughout Queensland, New South Wales and the Northern Territory.

Observations on the "gallery"

Various authors describe O. genoveva and O. zosine larvae sheltering in the "ants' nest" (Common and Waterhouse 1981, D'Abrera 1971, Fisher 1995, Kitching 1991, Nielsen and Common 1991) whilst McCubbin (1971) and Fisher (1978) describe the situation as ant "galleries". During the course of this investigation, over 100 colonies of O. genoveva and 40 colonies of O. zosine were examined. It was noticed that the Ogyris larvae were not

sheltering in the ants' "nest", ie. "a place used by insects....or the like for depositing their eggs or young" (Macquarie English Dictionary). The ants' nest was always located separately and sometimes quite a distance (5 m or more) from the "gallery" prepared by ants for the Ogyris larvae. In situations where the ants' nest was located near the base of the tree, O. genoveva larvae were kept in their specially prepared galleries well away from the ant brood. Therefore, it is suggested that the correct term to describe the excavated cavity where Camponotus ants attend O. genoveva and O. zosine larvae should be "gallery".

Both species of *Ogyris* shelter in naturally occurring situations such as borer holes, including those made by *Endoxyla* spp. (Lepidoptera: Cossidae), under suitable slabs of bark (Waterhouse 1913, Kitching 1991), in hollow branches and tree trunks (Waterhouse and Lyell 1908, McCubbin 1971, Le Souëf 1976), or even in an abandoned bird's nest (J. Olive, pers. comm.). Both *Ogyris* spp. larvae utilise these natural situations when available (see also DeBaar 1994), even when colonies on nearby trees are in galleries and soil conditions are suitable.

Camponotus ants were occasionally found renovating old galleries or constructing new ones without larvae present. Presumably there were eggs on the tree or small larvae on the mistletoes because on subsequent examination O. genoveva larvae were present in the gallery. The ants may excavate a number of chambers in the gallery that are not used by O. genoveva larvae. Some of these vacant chambers are later occupied by O. genoveva pupae, while others are sealed off and may contain dead O. genoveva larvae (see also McCubbin 1971). Galleries are usually around 15-20 cm deep but may be deeper (e.g. 30 cm or more).

In North Queensland, O. zosine larvae were observed attended by C. subnitidus Mayr, which nests in hollow branches or constructs an arboreal nest using accumulated debris. However, the ants still constructed galleries at the base of the tree for immature O. zosine. Many of these galleries were different from those constructed for O. genoveva, being closer to the surface and assembled with more cemented material such as leaves, rolled bark and other deposits. Gallery design varied according to terrain, weather conditions and available materials and, to a lesser extent, the ant species.

Ant behaviour

Of the four species of sugar ant encountered in the study site near Grafton, the behaviour of *C. intrepidus* was studied most thoroughly. It is a robust, easily provoked ant, with majors capable of inflicting a painful bite. *C. intrepidus* is darker than most other species of *Camponotus*, having a redbrown to black head, deep red-brown thorax and black abdomen. When there are thousands of these ants guarding a large colony of *O. genoveva* they can be quite a daunting adversary to any creature looking for an easy meal.

Some Camponotus and species are not openly aggressive, even when handled. By contrast, C. intrepidus were observed to quickly attack or repel arthropod predators or intruders such as tree crickets (Orthoptera: Gryllacrididae) or huntsman spiders (Araneida: Sparassidae). When danger threatens, ants herd O. genoveva larvae to the lower levels in the gallery by gently nipping the larvae to encourage them to move, occasionally picking them up or dragging them down the gallery. Significant disturbances can result in dramatic behavioural changes, whereby both C. intrepidus and C. consobrinus fiercely attack anything that interferes with the gallery. While in this aggressive state, Camponotus ants will even bite and kill dislodged O. genoveva and O. zosine pupae or larvae. Such ant frenzy is very short lived. By contrast, C. nigriceps and C. eastwoodi, when threatened, appeared to scatter and seek shelter. This passive behaviour was reflected in the higher rate of parasitism by braconid wasps, 100% (all 7 larvae) in the small colony attended by C. eastwoodi. Parasitism rate in the largest C. intrepidus attended colony was about 5% (8 out of approximately 150). Turner and Hawkeswood (1992) noted a parasitism rate of 32% in two colonies of O. genoveva attended by C. consobrinus.

Meat ants Iridomyrmex purpureus (Fr. Smith) prey upon the larvae of Ogyris (Samson and O'Brien 1981, Thorn 1924) and, when meat ants are present, less aggressive Camponotus species such as C. nigriceps and C. eastwoodi will reduce the size of the gallery entrance to a hole just big enough for two majors' heads to block and defend against any intruder. Occasionally C. nigriceps and C. eastwoodi completely seal up the gallery entrance with cemented soil and debris, especially when meat ants threaten, or sometimes during wet weather. C. intrepidus was not observed to be harassed by meat ants nor did they close their gallery entrance.

Any ants that die or any other ant intruders that are killed are carried some 10-15 cm away from the gallery entrance and dumped. A small dark species of ant (unidentified) was observed to take advantage of the graveyard food source by setting up a nest in close proximity to the *O. genoveva* gallery entrance. *O. genoveva* larval frass is similarly removed from the gallery (see Burns and Rotherham 1969). Frass is grabbed as it is being expelled, even when the *O. genoveva* larvae are feeding. At this point larval frass is usually carried a short distance and dropped.

Most food collected on the host tree by *Camponotus* ants is taken directly back to the ants' nest. However, when termites are swarming the ants have been observed to store a small number of them in an unoccupied gallery.

At Eatonsville, *C. intrepidus* construct their nest on exposed ground and cover the entrance during the day with cemented soil and debris. About an hour before sunset the nest entrance is opened and ant activity increases until after dark when ants can be seen foraging over a wide area. Peak ant activity is just after dark, when a constant stream of ants can be seen moving from the

nest across the ground into the gallery and from there up the tree. Initially, ant scouts proceed up the tree to the mistletoe well ahead of *O. genoveva* larvae, clearing off any predators along the way. Ants regularly stand guard on either side of the *O. genoveva* larval procession up the tree and especially on the return journey. Less attention is paid to the small larvae while larger larvae are constantly attended, with ants incessantly touching and stroking over the entire dorsal surface of the larvae with their antennae. Ants have also been observed gently pressing their open mandibles onto the dorsal ridge of larger *O. genoveva* larvae and riding on the backs of larvae as they crawl up the tree. Ants continually occupy the gallery even when all *O. genoveva* larvae are out feeding. On one occasion, ants from two *C. intrepidus* nests (presumably a polydomous colony) were observed entering the same gallery to attend *O. genoveva* larvae.

Ogyris larval behaviour

Ogyris genoveva larvae accumulate just inside the gallery entrance before dusk until the light level is sufficiently reduced for them to proceed. First and second instar larvae usually emerge first, heading straight up the tree, while some of the larger larvae linger outside the gallery entrance before continuing. Most O. genoveva larvae have emerged from the gallery within the first hour after sunset, with stragglers continuing to move up the tree until around 2130h EST. Larvae always follow the same route up the tree while laying down a fine silk thread and in larger colonies this trail can be clearly visible (Common and Waterhouse 1981). The larvae begin returning to the gallery around 0200h EST and continue until just after sunrise, with the majority returning before dawn.

Whenever O. genoveva and O. zosine larvae are active, either in transit or feeding, their tentacular organs are repeatedly everted (Samson 1987) whilst being attended by the ants. Ballmer and Pratt (1991) noted that the eversible organs apparently release chemicals which mimic ant alarm pheromone(s), inducing heightened activity and aggressive posturing in the attendant ants. However, these tentacular organs are rarely everted by O. genoveva or O. zosine larvae when they are in the gallery. This observation lends support to Ballmer and Pratt's contention, since Ogyris larvae would not require an aggressive response inside the gallery. Inside the gallery individual ants, in a torpid condition, often stand astride a pupa or larva and continuously monitor the pupal or larval extremities with their slowly moving antennae.

First instar O. genoveva larvae are often found in the gallery with other instars (they are easily overlooked). However, when the soil is waterlogged or when other ant species dominate the substratum, most smaller O. genoveva larvae group together under the base of the mistletoe while larger larvae shelter opportunistically in suitable situations.

To account for large numbers of Ogyris in a gallery it has been suggested that the ants may collect young Ogyris larvae from several trees and bring them

to a single gallery (Common and Waterhouse 1981). This was not observed during the study and is thought to be unlikely. Some large O. genoveva and O. zosine colonies may be surrounded by trees with separate colonies, often with a different species of Camponotus in attendance. In addition, a gallery of more than 200 individuals of O. genoveva and an abandoned bird nest containing more than 250 individuals of O. zosine have been observed in situations completely isolated from other trees. It is more likely that large larval numbers result from Ogyris females being drawn to a particular mistletoe by the presence of ants or other oviposition cues. Conversely, in the wet season, there are sometimes a larger number of host trees utilised by O. genoveva, each with only very small numbers of larvae (ca. 1-4) present. O. genoveva larvae are usually found under the bark at this time but in well drained areas will be found in small galleries at the base of the tree (see also Atkins 1993).

Ogyris genoveva larvae do not feed gregariously but spread out all over the mistletoe, feeding on the edges of the leaves and on new shoots. They feed for short periods punctuated by occasional intervals on the mistletoe stem. If mistletoe leaves are in short supply, larvae will eat the bark off the mistletoe stems.

Pupation usually occurs close to the entrance, within the gallery, on hard surfaces such as the tree trunk, on the sides of or under rocks or on partly buried bark. If suitable pupation sites are not available near the surface Ogyris will pupate further down under the tree roots. Destruction of O. genoveva pupal shells after emergence as reported by Common and Waterhouse (1981) was not observed, however, very few O. genoveva pupal remains were found.

Ogyris genoveva and O. zosine adults were mostly observed to emerge between 0730-0930h EST. The imago moves slowly after emerging from the pupa and expands its wings inside the gallery. Ants continue to monitor the almost motionless adult by gently tapping it alternately with their antennae. The attendant ants are generally in a very quiescent state but will occasionally crawl over the head and expanding wings of the motionless butterfly. When the butterfly's wings have hardened it walks slowly, stopping momentarily when approached by an ant, until it emerges from the gallery entrance. In confined pupation sites (eg in borer holes or under bark), the imago expands its wings as close as possible to the exit, usually in the company of ants. Ants vacate the gallery after all O. genoveva adults have emerged.

Unattended larvae or pupae were observed on three occasions. A single pupa was found under bark at Leyburn, Qld. One prepupal and one first instar O. genoveva larva were found sheltering under bark in the study area at Eatonsville, close to three O. oroetes Hewitson pupae being attended by a Crematogaster sp. ant. Similarly, an unattended pupa of O. zosine together

with numerous empty pupal shells was found under bark at Woodstock, west of Townsville, Old.

Discussion

Ogyris genoveva and O. zosine larvae benefit greatly from their association with the Camponotus ants. The ants are constantly attending the larvae or actively patrolling close by, protecting their symbionts from predators and parasitoids. In addition, ants expend enormous amounts of energy preparing and maintaining the galleries. The larvae of both Ogyris spp. appear to manipulate the degree of protection and attention that the ants bestow on them by regulating the release of chemicals from their tentacular (and other) organs according to their needs. However, studies have shown that the ants too profit from the association (see Fiedler and Saam 1995, Cushman et al. 1994, Pierce et al. 1987).

The ultimate survival of *O. genoveva* and *O. zosine* is, probably, dependent upon the attendant ants, for without them the larva would be exposed to formidable pressures from predators, parasitoids and the environment.

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